A METHOD FOR RECORDING AND ANALYZING VARIATIONS OF INTERNODE PATTERN

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This paper is an attempt "to make measurable that which has not yet been measured," the general habit of a plant. Those systematists who are also good field naturalists are often intrigued by the fact that closely related species of plants are commonly recognizable, even at a distance, by their peculiarities of habit, which are often more reliable than any single characteristic. But habit is difficult to convey to others and difficult to phrase concisely for a key or a technical description. It is based upon a number of things: the size, shape, positions, and textures of the leaves and the internode patterns of the vegetative shoot and the inflorescence. This paper provides an objective means for the analysis of variation in the latter.

Closely related species of the higher plants frequently differ in their internode pattern. That is to say, they may differ from each other not only in the number of internodes and their absolute dimensions but in the relative sizes of successive internodes and *in the pattern of change of relative size.* Unfortunately, there is usually so much variation from plant to plant that examination alone will not suffice to reveal the more or less constant tendencies which are being obscured by individual variation. Differences in internode pattern are apparently brought about largely by growth-regulating influences (of which auxin is certainly only one of several) which proceed from the root, from the stem apex, from leaves, flowers and fruits. The distribution of these substances is under such an internally correlated control system that successive internodes frequently become increasingly smaller or larger in an exact fashion and the increase or decrease may be described in mathematical terms (Prat, '35).

Before internode patterns can be studied, either as an interesting phenomenon in their own right or as a tool in taxonomic, genetic, and physiological investigations, we need a technique for recording and analyzing them. A simple method is presented below which overcomes the inadequacy of the human eye in perceiving rates of change. In fig. 1, for example, there are diagrammed the internodes of four hypothetical stems, A, B, C, and D. Two of these have fundamentally different growth patterns, though that fact will be apparent to relatively few biologists when the data are presented in this fashion. Almost any observant person will immediately note the differences in absolute length and in number of internodes. Most biologists will see the various differences in proportion. Few or none will note the fundamental change in proportion. In all four stems the internodes are getting increasingly larger but in A and B the increment is itself increasing while in C and D it is decreasing. If, however, we measure the lengths of successive internodes and diagram them from a common base line as in fig. 2, and then connect these points with straight lines for the eye to follow, the change in rate of increase is immediately apparent. A and B produce a fundamentally different curve from C and D.

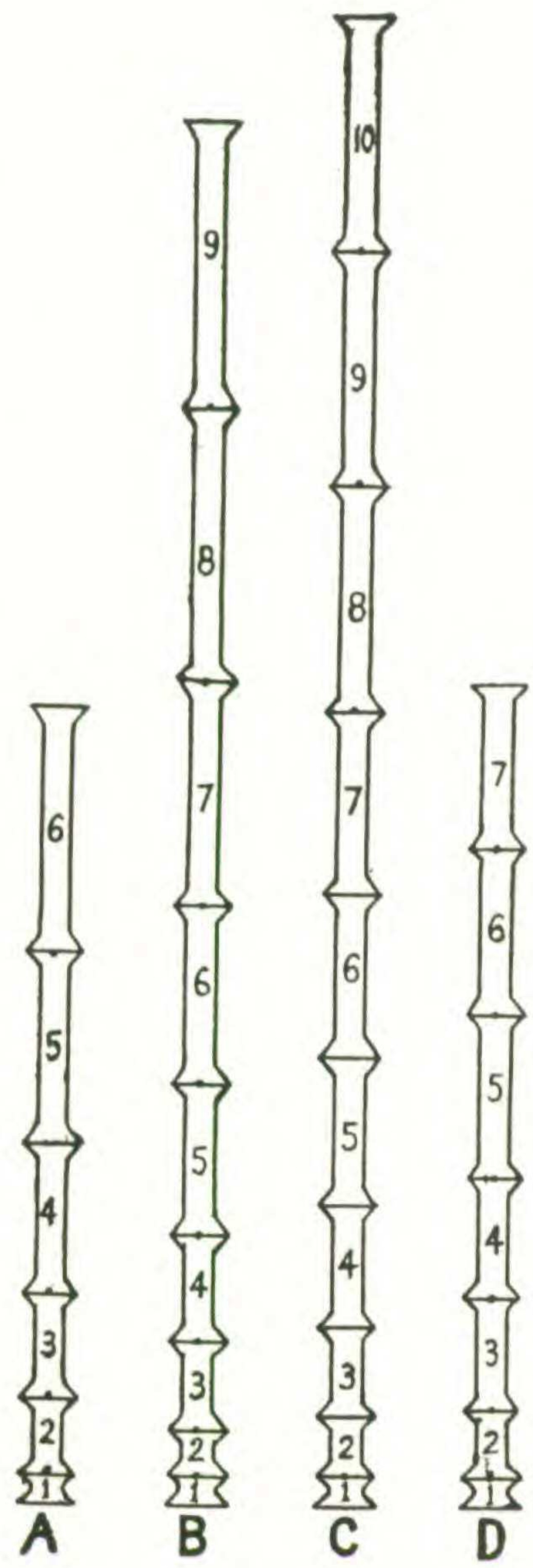

Fig. 1. Nodes and internodes of four hypothetical plants represented diagrammatically but to scale. The internode patterns of A and B are fundamentally different from those of C and D.

The use of logarithmic scales will immediately suggest itself to students of dynamic morphology. Prat ('35) has been successful with this method in analyzing the growth patterns of grass culms, and there are certainly many other kinds of material to which it might be applied. However, the internode patterns of plants are so various and many of them may be of such complexity that some simple method such as that outlined above should be tried out in each case until the fundamental facts have been established.

The internode pattern differences of two species of *Tradescantia* are illustrated in fig. 3. The method of fig. 2 has been extended by using circles to represent inflorescences and broken lines to represent secondary branches of the main stem (for a more elaborate representation of branching see below). The diagrams were prepared from herbarium specimens, and the small internodes at the base of the stem were ignored, though their pattern is also significant. Figure 3 shows that

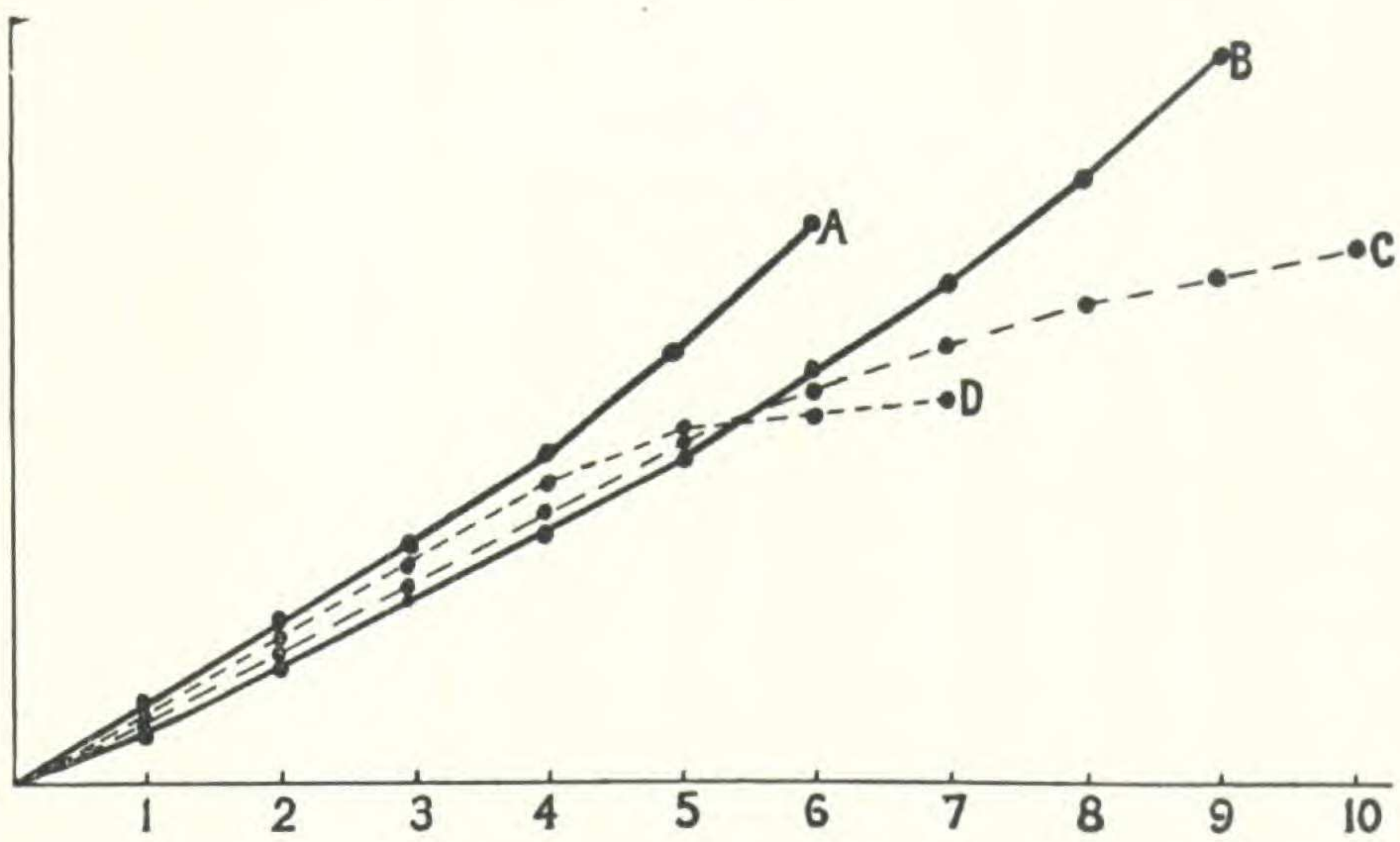

Fig. 2. The data of fig. 1 represented as internode diagrams. Vertical scale, length of internode; horizontal scale, successive internodes. The fundamental difference between A & B and C & D is immediately apparent.

the internode patterns of the two species present a number of out-and-out differences and an even larger number of tendencies to differ. The following are readily demonstrated:

1. *T. subaspera typica* has more internodes.

2. The longest internodes on *T. canaliculata* are usually longer than the longest on *T. subaspera typica*.

3. *T. subaspera typica* has 1 or 2 nodes of increasing magnitude at the base of the stem; *T. canaliculata* has 2 to 5.

4. The terminal internodes of *T. subaspera typica* decrease regularly in length. The decrease is so regular that the graph tends very strongly to be a straight line and might be described mathematically in exact terms. *T. canaliculata* has no such tendency; the terminal internodes may or may not be somewhat shorter than those preceding them.

The diagrams of fig. 3 illustrate several other significant points. *T. canaliculata* is a ubiquitous weed over a wide territory (Anderson and Woodson, '35). It includes a number of more or less differentiated races or sub-species which were once probably quite distinct but whose characters and distributions have been greatly modified by civilization (Anderson and Hubricht, '38). The three diagrams in the center of the figure represent one of these vaguely defined races in Texas and Oklahoma. *T. subaspera typica* and *T. canaliculata* sometimes hybridize when man so distorts the natural balance of things that hybrids can be produced and can find an intermediate habitat in which to survive (Anderson and Hubricht, '38,

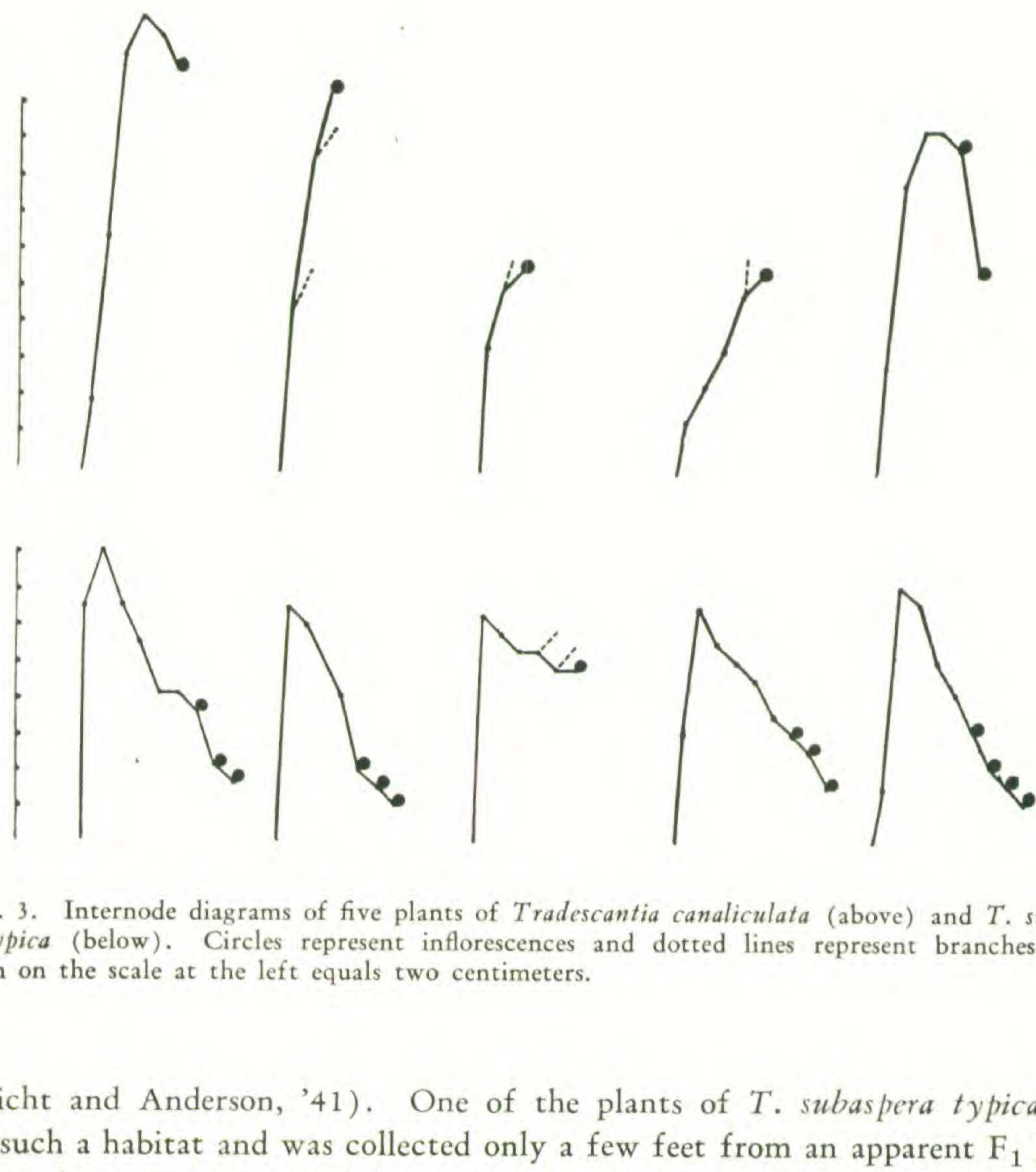

Fig. 3. Internode diagrams of five plants of *Tradescantia canaliculata* (above) and *T. subaspera* var. *typica* (below). Circles represent inflorescences and dotted lines represent branches. Each division on the scale at the left equals two centimeters.

Hubricht and Anderson, '41). One of the plants of *T. subaspera typica* came from such a habitat and was collected only a few feet from an apparent F_1 hybrid between the two species. While in its other characters it shows little influence of *T. canaliculata*, its internode pattern is so different that several biologists who have been shown these diagrams have been able to pick out the plant immediately. It is the third from the left in fig. 3.

Internode diagrams are particularly useful in analyzing such natural populations in which hybridization has occurred but in which it is not evident whether it is a blind alley or whether the variability of one or the other of the parental species is being enriched by back-crossing. Even in those cases where the parental species are so strikingly different that first-generation hybrids can be identified by inspection, it is a very difficult discipline so to train the eye that possible back-crosses can be distinguished. Unanalyzed variation in internode lengths gives the observer a vague impression as to the degree of variation but it usually does not answer the much more important question of its *direction.* Figure 4 illustrates a case in point, the hybridization between two species of Sage recently discussed by Epling ('44, pl. 4). Numerous individuals of both species and occasional undoubted

Fig. 4. Internode diagrams of two species of *Salvia* from Mt. Wilson, California, and a suspected back-cross hybrid. Same scale as fig. 3.

hybrids between them were studied along the Mt. Wilson road. At various points near well-established hybrids there were peculiar plants of *Salvia mellifera* but even Dr. Epling was unable to determine whether the variation was in the direction of S. *apiana,* as we would expect if the peculiarities were due to back-crossing.

Figure 4 suggests that the two species differ by the number of internodes below the flower, by the number of flowering nodes, and by whether the terminal internode is much longer than the one below it or of about the same size. It will be seen that in all of these characters the queer-looking individual departs from normal S. *mellifera* in the direction of S. *apiana.* The evidence from internode pattern would therefore suggest that it arose as a back-cross between S. *mellifera* and the first-generation hybrid which was growing near by. The internode diagrams (of which those in fig. 4 are a small sample) not only answered this question; they defined the internode differences between the two species so exactly that it was possible to study variation within and between these two species with a precision and an understanding hitherto impossible.

Sometimes the internode patterns of the secondary stems or of the inflorescences may be more significant than those of the main stem. They may then be diagrammed separately or combined in various ways. After a number of trials the technique shown in fig. 5 has apparently the widest applicability. It diagrams two plants each of two species of *Tripsacum.* The secondary branches are diagrammed from a new base line immediately above the node at which they originate and the tertiary branches from a still higher base line. The tertiaries of *T. Lemmoni* were too short at the time the measurements were made to register on the scale and are therefore indicated as short vertical lines of the approximate number of internodes.

The method described above might prove useful in a number of ways. Its prime importance will be to the student who is trying to understand specific or racial differences as well as to describe them. A monographer working in the field

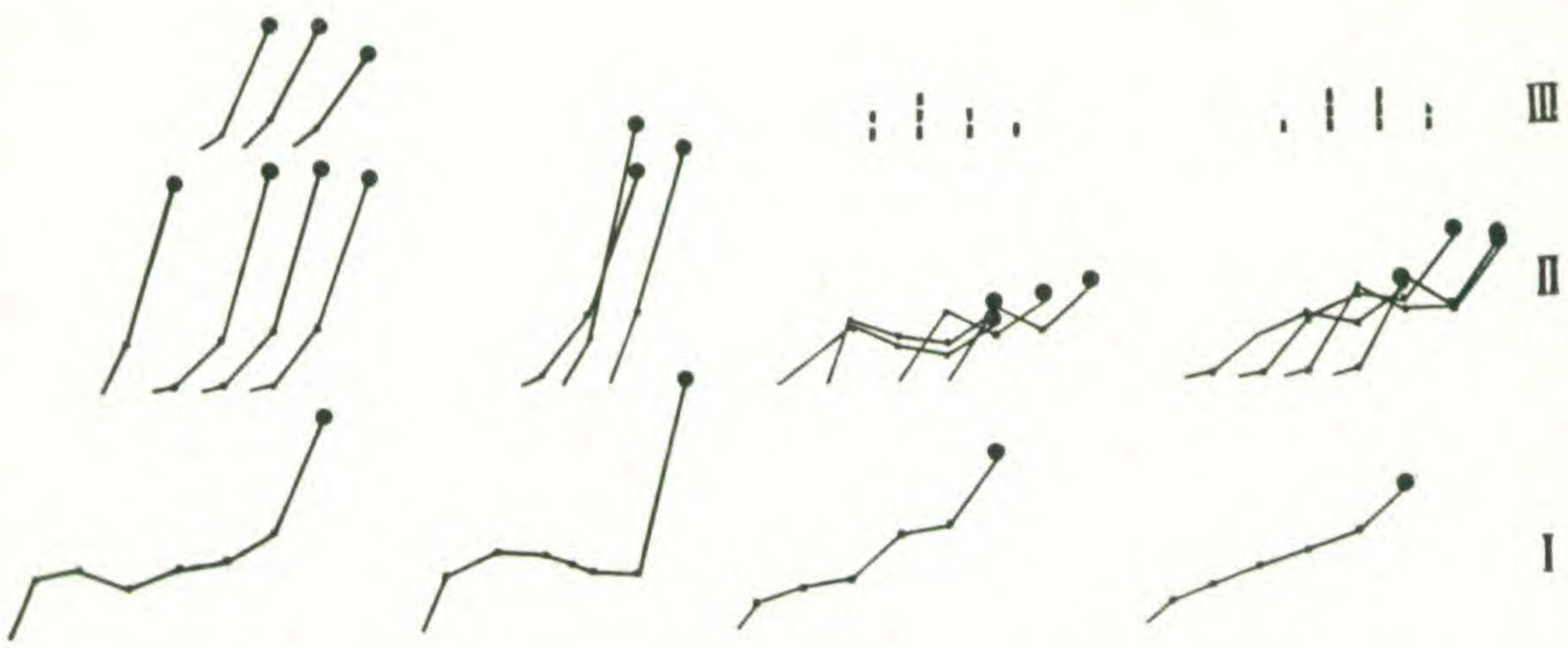

Fig. 5. Internode diagrams of two plants of *Tripsacum dactyloides* (left) and two of *T. Lemmoni* (right). Scale and construction as in figs. 3 and 4. The main axes of the four plants are diagrammed on line I, the secondary branches on line II and the tertiary branches (when present) on line III. The dotted lines for the tertiaries of *T. Lemmoni* represent short sterile branches of one to three nodes too short to be shown on the same scale as the rest of the diagrams.

of pure taxonomy would probably have little to learn from this method. Only in exceptional instances will it reveal a clear-cut specific difference which can be neatly phrased in a few words and incorporated in the description of a species or used in a key. However, the student of the species problem will find such characters as internode pattern of prime importance. His job is not merely to discriminate species but to illuminate them (Epling, '44, Anderson and Ownbey, '39, Anderson and Whitaker, '34). He must go beyond the cataloguing of a few outstanding differences and attempt to comprehend how the hiatus between two species came into being and how it is maintained. Internode patterns are reflections of internal growth-regulating systems. A comparison of patterns in different species or races may give us a real insight into the dynamics of these differences. The simple method outlined above may actually bring us closer to understanding fundamental physiological differences than would a series of chemical analyses. In this way it might be generally useful in various theoretical and practical problems.

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